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A review of the *Pseudomyrmex ferrugineus* and *Pseudomyrmex goeldii* species groups: acacia-ants and relatives (Hymenoptera: Formicidae)

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Abstract

The *Pseudomyrmex ferrugineus* group contains the Mesoamerican acacia-ants, an assemblage of species that inhabit and protect swollen-thorn acacias (*Vachellia* spp.). Recent phylogenetic studies have confirmed the existence of two generalist (dead twig-inhabiting) species that are embedded within the *P. ferrugineus* group. They are described here as *P. evitus* sp. nov. (occurring from Mexico to Costa Rica) and *P. feralis* sp. nov. (Guatemala). The morphological definition of the *P. ferrugineus* group is revised to incorporate additional variability in the worker and queen castes. The previous diagnosis of the males, based largely on features of the genitalia, requires little revision. Closely related to the *P. ferrugineus* group is a clade of five predominantly South American species, here designated and diagnosed as the *P. goeldii* group. The five species, *P. goeldii* (Forel), *P. laevifrons* Ward, *P. micans* sp. nov., *P. obtusus* sp. nov., and *P. parvulus* sp. nov., are characterized and illustrated. *P. laevifrons* and *P. micans* are closely related and difficult to distinguish, possibly reflecting incomplete isolation. Keys are provided for the identification of the species in both groups.

Key words: ants, ant-plants, Pseudomyrmecinae, taxonomy, Mesoamerica, South America

Introduction

Arboreal ants in the genus *Pseudomyrmex* are widely distributed in warm temperate and tropical regions of the New World, occurring from southern United States to Chile and Argentina. Most of the 200+ species are generalists, nesting in dead twigs or branches of a wide variety of plants, but about 40 species inhabit live domatia of specialized ant-plants (myrmecophytes) (Ward 1991; Ward & Downie 2005; Chomicki *et al.* 2015). The species living in domatia usually have a mutualistic relationship with their host, defending the plant from herbivores and plant competitors, and receiving shelter and sustenance in return (Janzen 1966; Benson 1985; Davidson *et al.* 1988; Ward 1991).

Probably the best known of these “plant-ants” are the members of the *Pseudomyrmex ferrugineus* group that occupy and protect swollen-thorn acacias (*Vachellia* spp.) of Mexico and Central America (Wheeler 1942; Janzen 1966, 1967, 1973; Kautz *et al.* 2009; Heil *et al.* 2009, 2014). These ants were revised taxonomically more than twenty years ago, with the consequent recognition of ten species (Ward 1993). Since that time no additional species of obligate acacia-ants have been discovered, but recent studies have revealed that two undescribed species of generalist twig-nesting *Pseudomyrmex* are nested phylogenetically within the *P. ferrugineus* group (Kautz *et al.* 2009; Chomicki *et al.* 2015; Ward & Branstetter, 2017). These two species are described herein and the definition of the *P. ferrugineus* group is updated to incorporate greater phenotypic variation in workers and queens. In addition, a cluster of five species that are closely related to the *P. ferrugineus* group is newly defined—as the *P. goeldii* group—and its constituent species are described and differentiated.

A brief explanation of the use of species groups is warranted. As employed here they are used to delimit groups of related species within a genus that can be recognized in some way. Unlike subgenera (or other cases of subordinate taxa within a larger taxon) there is no compulsion that all members of a genus—in which species groups are used—be assigned to a species group. Taxonomically isolated species or those whose affinities are unclear can be left by themselves, rather than being artificially pigeon-holed. Although species groups are informal and not regulated nomenclaturally, the viewpoint adopted here is that they should be monophyletic and mutually

exclusive. As knowledge of phylogenetic relationships improves this will require restructuring groups that are discovered to be non-monophyletic, as is done here (see also Ward 2017).

Materials and methods

As part of ongoing taxonomic studies on the subfamily Pseudomyrmecinae a large series of *Pseudomyrmex* specimens, encompassing all three castes (workers, queens, males), was examined for morphological variation. A subset of this material is relevant to the current study on the *P. ferrugineus* group and relatives. Most of the specimen records for acacia-ants have already been cited (Ward 1993; Chomicki *et al.* 2015, Table S8) and are not repeated here. Specimen records for new species (and new records of already described taxa) are documented below and come from the following collections:

ALWC	Alexander L. Wild Collection, Austin, TX, U.S.A
BMNH	Natural History Museum, London, U.K.
CASC	California Academy of Sciences, San Francisco, CA, U.S.A.
CPDC	Jacques Delabie Collection, CEPEC/CEPLAC, Itabuna, Bahia, Brazil
CUIC	Cornell University Insect Collection, Ithaca, NY, U.S.A.
FSCA	Florida State Collection of Arthropods, Gainesville, FL, U.S.A.
INBC	Instituto Nacional de Biodiversidad, San José, Costa Rica
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil
IZAV	Instituto de Zoológica Agrícola, Universidad Central de Venezuela, Maracay, Venezuela
JTLC	J. T. Longino Collection, University of Utah, Salt Lake City, UT, U.S.A.
KWJC	Klaus W. Jaffé Collection, Caracas, Venezuela
LACM	Los Angeles County Museum of Natural History, Los Angeles, CA, U.S.A.
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.
MHNG	Muséum d'Histoire Naturelle, Geneva, Switzerland
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MPEG	Museu Paraense Emílio Goeldi, Belém, Brazil
MUCR	Museo de Insectos, Universidad de Costa Rica, Costa Rica
MZLU	Museum of Zoology, Lund University, Lund, Sweden
MZSP	Museu de Zoologia da Universidade de São Paulo, Brazil
PSWC	P. S. Ward Collection, University of California at Davis, CA, U.S.A.
UCDC	Bohart Museum of Entomology, University of California at Davis, CA, U.S.A.
USNM	National Museum of Natural History, Washington, DC, U.S.A.
UVGC	Colección de Artrópodos, Universidad del Valle de Guatemala, Guatemala City, Guatemala

Many specimens (including all material from CASC, JTLC, PSWC and UCDC) have been assigned unique specimen codes, and the records have been uploaded to AntWeb (www.antweb.org). This includes type material of the new species. It should be noted, however, that most institutions listed above have not assigned specimen codes to their holdings. Hence the lists of “Material examined” under each species treatment provide more complete information about the distribution of each species than the records currently on AntWeb.

The measurements and indices employed in this study are listed below (see also Ward 1985, 1989, 1993). All linear measurements are in millimeters.

HW	Head width: maximum width of head, including the eyes.
HL	Head length: midline length of the head capsule, measured in full-face (dorsal) view, from the anterior clypeal margin to the midpoint of a line drawn across the posterior margin of the head; concavities at either end do not reduce measurement.
EL	Eye length: length of the compound eye, measured with the head in full-face view.
MFC	Minimum frontal carinal distance: minimum distance between the frontal carinae, posterior to their fusion with, or approximation to, the antennal sclerites.

SL	Scape length: length of first antennal segment, excluding the radicle.
FL	Profemur length: length of the profemur, measured along its long axis in posterior view (Ward 1985, fig. 3).
FW	Profemur width: maximum measurable width of profemur, measured in the same view as FL, perpendicular to FL.
PL	Petiole length: length of the petiole, measured in lateral view, from the lateral flanges at the anterior end of the petiole to the posterior extremity of the petiole (Ward 1985, fig. 4).
PH	Petiole height: maximum height of the petiole, measured in lateral view perpendicular to PL, but excluding any protruding anteroventral or posteroventral processes.
DPW	Dorsal petiole width: maximum width of the petiole, measured in dorsal view.
LHT	Metatibia length: length of the metatibia, measured in dorsal view, orthogonal to the plane of tibial flexion and excluding the proximomedial portion of the articulation with the metafemur (Ward 1989, fig. 5).
CI	Cephalic index: HW/HL
REL	Relative eye length: EL/HL
REL2	Relative eye length, using head width: EL/HW
FCI	Frontal carinal index: MFC/HW
SI	Scape index: SL/HW
FI	Profemur index: FW/FL
PLI	Petiole length index: PH/PL
PWI	Petiole width index: DPW/PL
MSC	Mesosomal setal count: number of standing hairs, i.e., those forming an angle of 45° or more with the cuticular surface, visible in outline on the dorsal surface of the mesosoma.
HTC	Metatibial setal count: number of standing hairs visible in outline on the outer (extensor) surface of the metatibia.
MTC	Mesotibial setal count: equivalent setal count for mesotibia.

Terms for surface sculpture follow Harris (1979). Descriptions of integument sculpture and reflectance are based on observations made with soft (fluorescent) lighting. The palp formula refers to the number of maxillary palp segments followed by the number of labial palp segments. 5p4,3 indicates a condition intermediate between 5,3 and 4,3, in this case due to partial fusion of the fourth and fifth maxillary palp segments. Terminology for wing venation is taken from Gauld & Bolton (1988) and Yoshimura & Fisher (2012).

Results

Provisional key to *Pseudomyrmex* species groups, based on the worker caste

The primary purpose of this key is to permit recognition, within the ant genus *Pseudomyrmex*, of the *P. ferrugineus* group, *P. goeldii* group, and closely related species (Fig. 1); such taxa are highlighted in **bold font** in the key. Species groups have been modified from those recognized in Ward (1989), to reflect more recent knowledge of phylogenetic relationships (Ward & Downie 2005; Chomicki *et al.* 2015; Ward 2017). The key also includes taxonomically isolated species that are unplaced to a group.

- 1 Frontal carinae closely contiguous, elevated anterodorsally, and directed forward onto the median clypeal lobe rather than fusing anterolaterally with the antennal sclerites (Fig. 7a; see also Ward 1989, figs. 18–19) 2
- Frontal carinae variably separated, not elevated anterodorsally, directed anterolaterally and fusing with the antennal sclerites (Fig. 2a; see also Ward 1989, figs 16–17) 3
- 2 Median clypeal lobe laterally angulate (Fig. 7a); head moderately elongate (CI 0.69–0.85); standing pilosity lacking on propodeum **goeldii group**
- Median clypeal lobe laterally rounded; head usually more elongate (CI 0.56–0.73); a pair of long hairs present at the juncture of the dorsal and declivitous faces of the propodeum **subtilissimus group**
- 3 Standing pilosity moderately common to abundant on most parts of body, including mesosoma dorsum (Fig. 2b); MSC usually >12, but if slightly less (7–12) then the standing hairs scattered and mostly shorter than the maximum dorsoventral width of the metatibia 4

- Standing pilosity sparse on most of body, the hairs on mesosoma dorsum typically arranged as 1–2 and 0–1 isolated pairs on the pronotum and propodeum, respectively; MSC usually <8; very rarely (some *sericeus* group species; see characterization of the group in couplet 23) MSC 8–12 as a result of additional hairs on the pronotum and mesonotum, but in that case hairs tending to occur as isolated pairs, whose length exceeds the maximum dorsoventral width of metatibia 22
- 4 Large species (HW 1.38–1.90) with opaque head and relatively small eyes (REL 0.42–0.46); pronotum with pronounced lateral margination; metanotal groove lacking or very weakly impressed; palp formula 6,4; confined to southern Mexico and northern Central America *rufomedius* group
- Size and head sculpture variable but if HW >1.35 then either eyes more elongate (REL >0.48) and/or pronotum laterally rounded; metanotal groove generally well developed; palp formula variable; widespread 5
- 5 Standing pilosity common on the outer (extensor) surface of the mesotibia and metatibia, (HTC + MTC)>10; the tibial hairs usually long and conspicuous with their maximum length being subequal to, or greater than, the maximum dorsoventral width of the tibia (sometimes hairs shorter, but still distinct from background pubescence, if latter present) 6
- Tibial pilosity sparse, (HTC+MTC) usually <8 but if greater then hairs inconspicuous and tending to grade into a background of appressed and subdecumbent pubescence 11
- 6 Propodeum depressed downward, the dorsal and declivitous faces essentially undifferentiated and appearing in profile as a single convex slope, which contacts the propodeal spiracle; head smooth and shiny, with widely scattered punctulae *depressus* (Forel)
- Propodeum not depressed downward, the dorsal and declivitous faces differentiated; propodeal spiracle situated on the side of the propodeum, below the level of the propodeal dorsum; head variable, usually more densely sculptured 7
- 7 Eyes elongate, more than half the head length (REL 0.52–0.67); petiole usually slender, width rarely as much as three-quarters of the length (PWI 0.34–0.75); palp formula 6,4 *gracilis* group (except *simulans*)
- Eyes relatively short, less than half the head length (REL 0.32–0.48); petiole usually broader (PWI 0.66–1.40); palp formula variable 8
- 8 Head notably broader than long (CI 1.08–1.16); compound eye located on the posterior third of head; body pilosity long and abundant, MSC approximately 95–150, HTC 25–50 *kuenckeli* (Emery)
- Head usually longer than broad, less commonly as broad as long (CI 0.70–1.04); compound eye positioned about the middle of the side of the head; body pilosity less abundant, MSC <90, HTC <25 9
- 9 Scape and funicular segments very short (SI 0.39–0.43); punctures on upper third of head sparse, of uneven density, mostly small and separated by many diameters, leaving extensive smooth interspaces; palp formula 4,3; *Tachigali* inhabitants *concolor* group (except *tachigaliae*)
- Scape and funicular segments longer (SI 0.42–0.50); punctures on upper third of head moderately dense, uniformly dispersed, most punctures separated by one to several diameters; palp formula 6,4 or 5,3; nesting in dead stems, live stems, or domatia, but not in *Tachigali* 10
- 10 Smaller species, HW (0.73–0.94); petiole relatively slender (DPW/HW 0.32–0.39, DPW/LHT 0.40–0.46); Mexico to Costa Rica *servidus* group (except *hesperius*)
- Larger species, on average (HW 0.74–1.51); if HW <0.95 then petiole broader (DPW/HW 0.39–0.50, DPW/LHT 0.48–0.58); widespread, mostly in South America *triplarinus* group
- 11 Median clypeal lobe laterally angulate (Fig. 2a) 12
- Median clypeal lobe laterally rounded 14
- 12 Petiole relatively short (PLI 0.72–0.82), lacking anterior peduncle; *Tachigali* inhabitant *tachigaliae* (Forel) (*concolor* group)
- Petiole more elongate (PLI 0.47–0.70), with weakly to strongly differentiated anterior peduncle; nesting habits variable, not *Tachigali* inhabitant 13
- 13 Small species (HW 0.78–0.86), with very elongate eyes (REL 0.60–0.62) and robust profemur (FI 0.48–0.53); nesting in dead twigs *oki* (Forel) (*pallidus* group)
- Larger species (HW 0.94–1.26), with less elongate eyes (REL 0.42–0.55) and more slender profemur (FI 0.35–0.46); nesting habits variable, most species inhabiting swollen-thorn acacias (*Vachellia*) *ferrugineus* group (part)
- 14 Standing pilosity present on the proximal funicular segments and (as numerous rather short and inconspicuous hairs) on the outer surface of the mesotibia and metatibia; body pubescence thick and partly decumbent giving worker a “scruffy” appearance; eyes relatively short (REL <0.50); anteroventral postpetiolar process well developed *subater* (Wheeler & Mann) (*duckei* group)
- Without the preceding patterns of pilosity; if body pubescence conspicuously thick and decumbent then eyes more elongate (REL >0.50) and anteroventral postpetiolar process not developed 15
- 15 Eyes elongate, about one half head length or more (REL 0.48–0.62); petiole relatively short and high (PLI 0.75–1.09); EL/PL 1.09–1.59; palp formula 6,3, reduced to 5,3 in the smallest species (HW <0.68) *oculatus* group
- Eyes shorter (REL <0.48) and/or petiole longer (PLI <0.71); EL/PL usually less than 1.05; palp formula variable, not 6,3 16
- 16 Head sublucid to lucid; sculpture on upper third of head between ocelli and compound eye consisting of scattered minute or medium-sized punctures separated by their diameters or more, the interspaces smooth, shiny and unsculptured 17
- Head opaque to sublucid, sculpture consisting of contiguous punctulae (separated by less than their diameters) or with punctulae separated by coriarious sculpture, smooth shiny interspaces largely lacking 19
- 17 Small species (HW 0.65–0.69) with relatively small eyes (REL 0.43–0.46) and a short apedunculate petiole (PLI 0.73–0.77); western Mexico *hesperius* Ward (*servidus* group)
- Larger species (HW >0.70) with more elongate eyes (REL 0.48–0.59) and longer petiole (PLI 0.50–0.69) 18
- 18 Head elongate (CI 0.75–0.82), eyes shorter (REL 0.48–0.53) and petiole longer (PLI 0.50–0.57); punctulae on head minute and

	inconspicuous, even under 50× magnification; palp formula 5,4	<i>filiformis</i> (Fabricius)
-	Head broader (CI 0.81–0.93) with longer eyes (REL 0.56–0.59) and shorter petiole (PLI 0.59–0.69); punctures on head variable, minute and sparse or conspicuous and dense; palp formula 6,4	<i>duckei</i> group (except <i>subater</i>)
19	Larger species (HW 1.22–1.34) with elongate eyes (REL 0.52–0.55); pronotum laterally submarginate; Panama	<i>simulans</i> Kempf (<i>gracilis</i> group)
-	Smaller species (HW 0.74–1.21); eye size variable (REL 0.40–0.57); pronotum laterally rounded; widespread	20
20	Frontal carinae closely contiguous, separately by less than basal scape width (FCI 0.022–0.045); palp formula 6,4; usually nesting in dead twigs; predominantly South American in distribution	21
-	Frontal carinae less closely contiguous, usually separated by about basal scape width (FCI 0.042–0.101); palp formula 5,3 or 4,3; nesting in swollen-thorn acacias (<i>Vachellia</i>); restricted to Mesoamerica	<i>ferrugineus</i> group (part)
21	Eyes shorter (REL 0.45–0.46) and petiole longer (EL/PL 0.82–0.84); endemic to western Mexico	undescribed species (<i>elongatulus</i> group)
-	Eyes longer (REL 0.47–0.57) and petiole shorter (EL/PL 0.91–1.20); distributed from Costa Rica to Brazil and Argentina	<i>pallens</i> group (part)
22	Median clypeal lobe laterally rounded	23
-	Median clypeal lobe laterally angulate (as in Fig. 2a)	27
23	Masticatory margin of mandibles with 8–10 teeth or denticles; body covered with a very fine appressed pubescence, giving the integument a silky appearance; eyes very long (REL 0.56–0.70); petiole short, high, and broad (PLI 0.86–1.26)	<i>sericeus</i> group
-	Masticatory margin of mandibles with 5–6 teeth; without the combination of other characters	24
24	Head smooth, shiny, with scattered fine punctulae; metanotal groove deeply impressed	<i>perboscii</i> (Guérin)
-	Head subopaque to opaque, with densely punctulate or punctulate-coriarious sculpture; metanotal groove moderately impressed or absent	25
25	Large species (HW 1.16–1.42, LHT 1.01–1.28), with elongate eyes (REL 0.56–0.74); pronotal humeri subangulate	<i>tenuis</i> group
-	Smaller species (HW 0.62–1.20, LHT 0.58–1.05); eyes usually shorter (REL 0.39–0.58); pronotal humeri rounded	26
26	Eyes smaller, on average (REL 0.48–0.60); endemic to Mesoamerica (Mexico to Costa Rica)	<i>elongatulus</i> group (part)
-	Eyes larger, on average (REL 0.52–0.75); endemic to South America	<i>pallens</i> group (part)
27	Masticatory margin of mandible with 6 teeth; palp formula 6,3; endemic to Hispaniola	<i>haytianus</i> (Forel)
-	Masticatory margin of mandible with 5 teeth; palp formula 5,3 or 4,3; widespread	<i>pallidus</i> group (part)

Pseudomyrmex ferrugineus group

A detailed morphological diagnosis of the *P. ferrugineus* group, based on the species then known, was given in Ward (1993: 133). Now that two additional species, described below, have been discovered to be part of the same clade (Fig. 1), a revised diagnosis is needed. This primarily affects the worker and queen castes, where allowance must be made for morphological differences between the mutualists (inhabiting *Vachellia* domatia) and generalists (nesting in dead twigs). The male diagnosis requires less revision, since features of the male morphology, including the genitalia, are evidently less variable across different life histories.

Worker diagnosis. Medium sized species (HW 0.74–1.28, HL 0.86–1.42); head varying from somewhat elongate to rather broad (CI 0.75–1.05); eyes moderately elongate in non-mutualist species (REL 0.48–0.55), shorter in the mutualist acacia-ants (REL 0.39–0.50). Masticatory margin of mandible with 6, rarely 7, teeth; mesial tooth on basal margin closer to apicobasal angle than to proximal tooth. Palp formula 5,3, reduced to 4,3 in three species. Anterior margin of median clypeal lobe somewhat blunt-edged, in dorsal view convex, straight or concave, laterally rounded or with sharp angles. Frontal carinae separated by about basal scape width in most species but more closely contiguous in some (FCI 0.03–0.10), fusing anterolaterally with antennal sclerites. Profemur relatively robust in non-mutualist species (FI 0.42–0.46), more slender in mutualist acacia-ants (FI 0.35–0.41). Pronotum laterally rounded. Metanotal groove weakly impressed in non-mutualists, well developed in mutualists. Basal and declivitous faces of propodeum moderately well differentiated and subequal in length, in profile the juncture between the two subangulate or gently rounded. Petiole relatively long (PL/HL 0.44–0.63), always much longer than high or wide (PLI 0.47–0.71, PWI 0.46–0.75), small anteroventral tooth present; in four species anterior peduncle of petiole weakly differentiated and posterolateral corners of petiolar node not expanded (the presumed plesiomorphic condition), in other species petiole with distinct anterior peduncle and with expanded, subangulate posterolateral corners. Postpetiole broader than long, with small anteroventral tooth. Body sculpture varying from densely punctulate or punctulate-coriarious to coriarious-imbricate, the integument sublucid to opaque; dorsum of head never with extensive smooth, shiny interspaces (punctulae usually separated by their

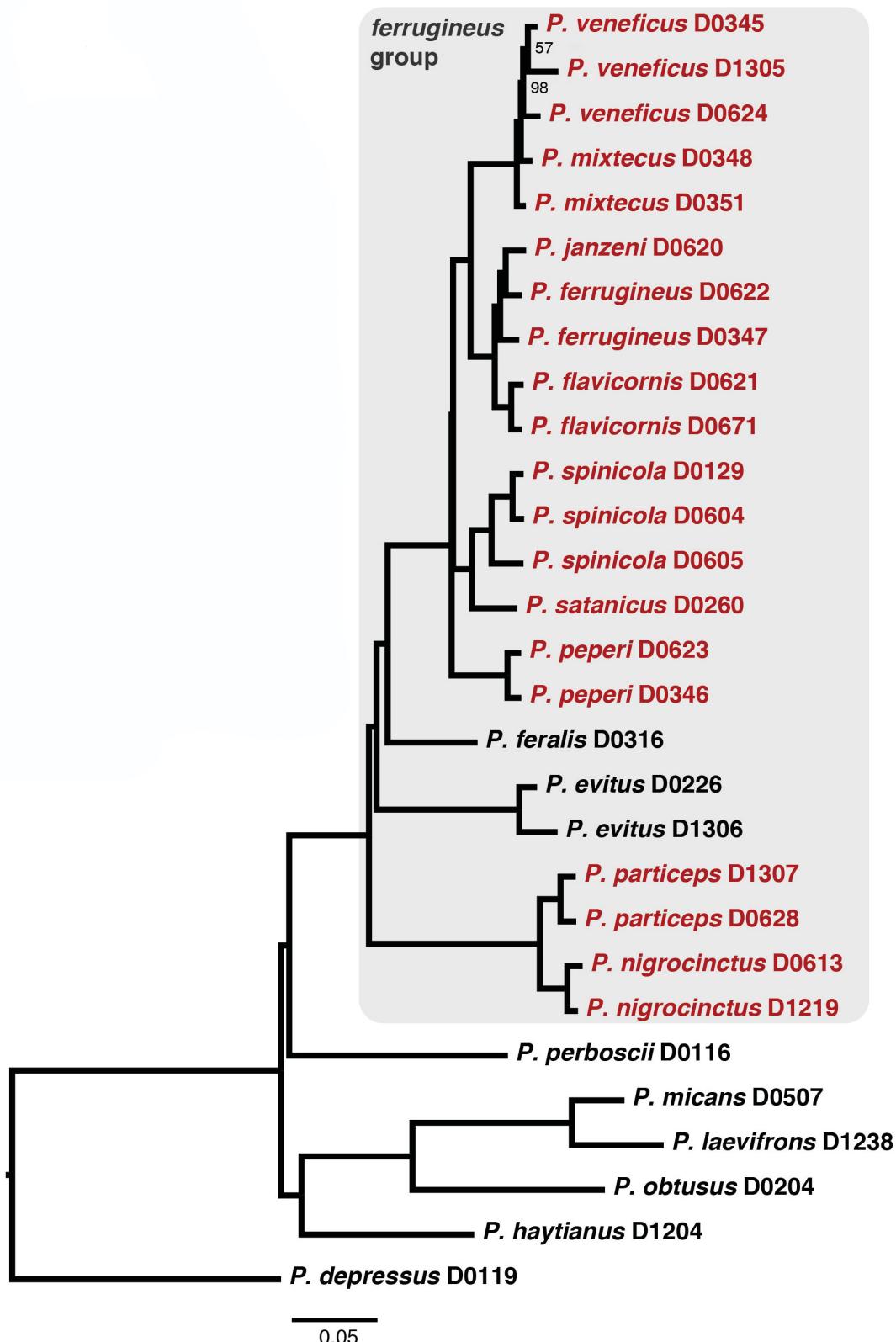


FIGURE 1. Phylogenetic relationships in the *Pseudomyrmex ferrugineus* group and related species, based on maximum likelihood (ML) analysis of 1,672 UCE (ultra-conserved element) loci (from Ward & Branstritter 2017). Bootstrap support is 100% at all nodes except the two whose support values are shown. Obligate acacia-ants are in red font, and can be seen to comprise two clades within the *P. ferrugineus* group. Two species (*P. ferrugineus*, *P. mixtecus*) are paraphyletic, consistent with a recent origin of their sister species by peripatric speciation (Ward & Branstritter 2017). The *P. goeldii* group is represented by three of its five species: *P. laevifrons*, *P. micans* and *P. obtusus*.

diameters or less); propodeum of some species overlain by a coarser but weak rugulo-punctate sculpture. Standing pilosity usually common, less abundant in non-mutualists (MSC 7–26) than mutualists (MSC 10–62), present on the scapes, head, mesosoma dorsum, petiole, postpetiole and gaster, absent from the extensor faces of tibiae (HTC 0, MTC 0). Appressed pubescence dense on most of body, including head and abdominal tergite IV. Color varying from light yellow- or orange-brown to black.

Queen diagnosis. Similar to worker except for caste-specific differences. Larger in size (HW 0.76–1.36, HL 1.00–1.81), head more elongate (CI 0.60–0.88). Median clypeal lobe narrower and more protruding, anterior margin convex or straight, laterally rounded or subangulate. Profemur robust in non-mutualists (FI 0.46–0.51), more slender in mutualists (FI 0.39–0.44). Petiole and postpetiole generally more slender than in worker (PL/HL 0.57–0.74, PLI 0.43–0.63, PWI 0.47–0.67). Forewing with 2 submarginal cells (erroneously called “cubital cells” in Ward (1993)), i.e., cross-vein 2rs-m present.

Male diagnosis. Head varying from longer than broad to slightly broader than long (CI 0.82–1.11 in a sample of 73 males belonging to all species); compound eye large, prominent (REL2 0.46–0.62). Mandibles with 8+ teeth or denticles on masticatory margin. Palp formula as in females, but somewhat more variable (males with 5p4,3 commoner than in workers or queens). Surface of median clypeal lobe convex, its anterior margin subtriangular in shape (dorsal view) with sides converging medially to a rounded point. Petiole and postpetiole more slender than in workers (PLI 0.39–0.55, PWI 0.35–0.51) and simpler in shape. Posterolateral corners of sternites IV–VIII not notably protruding ventrally. Subgenital plate (sternite IX) with a conspicuous posteromedial concavity. Posterior margin of pygidium (tergite VIII) convex, directed posteroventrally. Paramere with several characteristic features (Ward 1993: 134): a finger-like, posterodorsally directed mediodorsal lobe; angulate or expanded posterodorsal extremity; and mesial dorsoventral ridge which joins the mediodorsal lobe posteriorly. Aedeagus with expanded posterodorsal corner, a medial protrusion on the posterior margin, numerous small teeth (15+) on the posterior margin, and on the outer face a raised ridge curving posterodorsally from a basal origin.

List of included species

P. evitus Ward, sp. nov.; Mexico to Costa Rica

P. feralis Ward, sp. nov.; Guatemala

P. ferrugineus (F. Smith 1877); Mexico to Honduras

- = *P. belti fulvescens* (Emery 1890) (synonymy: Ward 1989)
- = *P. canescens* (Wasmann 1915) (synonymy: Ward 1989)
- = *P. wasmanni* (Wheeler 1921) (replacement name for *canescens*)
- = *P. belti bequaerti* (Wheeler 1942) (synonymy: Ward 1989)
- = *P. belti saffordi* (Wheeler 1942) (synonymy: Ward 1989)
- = *P. belti vesanus* (Wheeler 1942) (synonymy: Ward 1989)
- = *P. bequaerti* (Enzmann 1945) (synonymy: Brown 1949)
- = *P. kuenckeli honduranus* (Enzmann 1945) (synonymy: Ward 1989)

P. flavigaster (F. Smith 1877); Guatemala to Costa Rica

- = *P. belti* (Emery 1890) (synonymy: Ward 1989)
- = *P. belti obnubilus* (Menozzi 1927) (synonymy: Ward 1989)
- = *P. belti fellosus* (Wheeler 1942) (synonymy: Ward 1989)

P. janzeni Ward 1993; Mexico

P. mixtecus Ward 1993; Mexico

P. nigrocinctus (Emery 1890); Guatemala to Costa Rica

- = *P. alfarei* (Forel 1906) (synonymy: Ward 1993)
- = *P. nigrocinctus bicinctus* (Santschi 1922) (synonymy: Ward 1993)
- = *P. peltatus* (Menozzi 1927) (synonymy: Ward 1993)

P. particeps Ward 1993; Costa Rica

P. peperi (Forel 1913); Mexico to Nicaragua

- = *P. spinicola convarians* (Forel 1913) (synonymy: Ward 1989)
- = *P. satanicus saffordi* (Enzmann 1945) (synonymy: Ward 1989)

P. satanicus (Wheeler 1942); Panama

P. spinicola (Emery 1890); Honduras to Colombia

= *P. spinicola atrox* (Forel 1912) (synonymy: Ward 1993)

= *P. spinicola gaigei* (Forel 1914) (synonymy: Ward 1993)

= *P. spinicola infernalis* (Wheeler 1942) (synonymy: Ward 1993)

= *P. spinicola sclerosus* (Wheeler 1942) (synonymy: Ward 1993)

= *P. spinicola infernalis* (Enzmann 1945) (synonymy: Brown 1949)

= *P. spinicola sclerosus* (Enzmann 1945) (synonymy: Brown 1949)

P. veneficus (Wheeler 1942); Mexico

= *P. belti veneficus* (Enzmann 1945) (synonymy: Brown 1949)

Descriptions of new species

Pseudomyrmex evitus Ward, sp. nov.

(Fig. 2)

Pseudomyrmex sp. PSW-02; Ward (1993: 135). Male genitalia similar to those of *P. ferrugineus* group.

Pseudomyrmex psw002; Chomicki *et al.* (2015: 4). Nested phylogenetically in *P. ferrugineus* group.

Type material. Holotype worker. COSTA RICA Heredia: Est. Biol. La Selva, 50–150m, 10°26'N 84°01'W, Mar 1994 [in recent treefall, tropical rainforest], INBio-OET, J. Longino JTL03593 (INBC) (INBIOCRI001271962).

Paratypes. Series of 7 workers, same data as holotype (CASC, JTLC, INBC, PSWC, UCDC).

Other material examined. (BMNH, INBC, JTLC, MUCR, PSWC, UCDC, USNM). MEXICO Chiapas: Playón de la Gloria, 180m (LLAMA); Tabasco: Teapa (H. H. Smith); Veracruz: Estación de Biología Los Tuxtlas, 115 m (P. S. Ward); Los Tuxtlas, 10 km NNW Sontecomapan, 200 m (P. S. Ward); BELIZE Cayo: Las Cuevas, 5 km SE Millionario (C. Lyal & D. Hollis); GUATEMALA Petén: Tikal (T. H. Hubbell); Tikal Natl. Park, 270 m (J. Longino); HONDURAS Atlántida: Carmelina (W. M. Mann); Comayagua: PN Cerro Azul Meambar, 1170 m (LLAMA); COSTA RICA Heredia: 11 km ESE La Virgen, 300 m (ALAS); 2 km NW Pto. Viejo, 50 m (G. Gomez); 22 km N Volcan Barba, 500 m (J. Longino); Chilamate, 75 m (Hanson & Godoy).

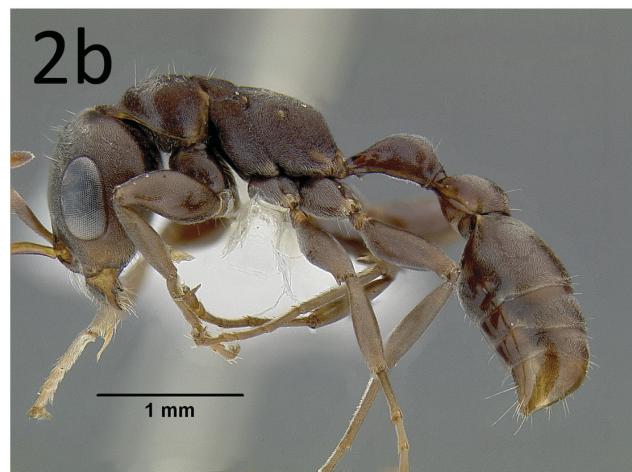
Worker measurements (n = 14). HL 1.13–1.25, HW 1.15–1.28, MFC 0.040–0.070, LHT 0.91–1.00, CI 1.01–1.05, REL 0.52–0.55, REL2 0.51–0.54, FCI 0.033–0.056, FI 0.42–0.45, PLI 0.49–0.56, PWI 0.50–0.60.

Worker diagnosis. Medium-sized species (see HL, HW and LHT measurements) with broad head (CI >1.00) and elongate eyes (REL >0.50); anterior margin of median clypeal lobe concave, and laterally angulate; palp formula 4,3; frontal carinae separated by less than basal scape width; profemur relatively robust; mesosoma as in Fig. 2b, metanotal groove weakly impressed; dorsal face of propodeum slightly longer than, and rounding into, declivitous face; petiole as in Fig. 2b, about twice as long as high or wide, anterodorsal face ascending gradually, without a well differentiated anterior peduncle; dorsal surface of petiole with a weak median furrow; postpetiole broad, about 1.6–1.7× petiole width. Head, mesosoma and petiole densely punctulate-coriarious and mostly opaque; postpetiole and abdominal tergite IV similarly opaque, their reflectance dulled by fine punctulae and associated dense pubescence. Standing pilosity fine, pale, and moderately common on most parts of the body (MSC 13–26), present on the mesonotum and (usually) propodeum. Dark brownish-black, the appendages medium brown.

Comments. This species is readily recognized by the combination of the shape of the clypeal lobe (medially concave and laterally angulate); broad head; dense coriarious-punctulate sculpture which renders the body opaque; and petiole shape (Fig. 2b). The reduced palp formula, elongate eyes, weakly impressed metanotal groove, and uniformly dark coloration are also distinctive. *P. feralis*, the other non-mutualist species in the *P. ferrugineus* group, is similar to *P. evitus* in the shape of the clypeus and mesosoma, but it is smaller (HW 0.94–0.99) with less heavily sculptured integument, shorter legs (LHT 0.73–0.77), and a more elongate head (CI 0.90–0.94). Males of *P. evitus* have an unusually elongate third (penultimate) segment of the maxillary palps, which is about 2.6× the length of the terminal segment.

Distribution and biology. *P. evitus* is an uncommon species, known from scattered locations from southern Mexico to Costa Rica. Collections come from tropical moist forest, lowland rainforest, lowland rainforest edge,

and montane rainforest, at elevations ranging from 50 m to 1170 m. I have encountered this species in the field only at Estación de Biología Los Tuxtlas, Veracruz, Mexico, where I found single foragers on the ground and on a tree trunk, and a nest in a dead twig. In contrast to the acacia-ants the workers of *P. evitus* have a timid disposition.



FIGURES 2–3. *Pseudomyrmex ferrugineus* group, workers, full-face dorsal view of head (a) and lateral profile of body (b). 2, *P. evitus*, Costa Rica (INBIOCRI001271962); 3, *P. feralis*, Guatemala (CASENT0794097). Images from AntWeb (www.antweb.org); photographer Matthew Prebus.

Pseudomyrmex feralis Ward, sp. nov.

(Fig. 3)

Pseudomyrmex sp. PSW-54; Ward (1993: 135). Male genitalia similar to those of *P. ferrugineus* group.

Pseudomyrmex sp. PSW-54; Kautz *et al.* (2009: 847). Nested phylogenetically in *P. ferrugineus* group.

Pseudomyrmex sp. PSW-54; Heil *et al.* (2009: 18093). Nested phylogenetically in *P. ferrugineus* group.

Pseudomyrmex psw054; Chomicki *et al.* (2015: 4). Nested phylogenetically in *P. ferrugineus* group.

Pseudomyrmex sp. PSW-54; Rubin & Moreau (2016: 3). Genome sequenced and compared with that of *P. flavigaster*.

Type material. Holotype worker. GUATEMALA Sacatepéquez: Parque Florencia, nr. San Miguel Milpas Altas, 1900 m, 14°34'N 90°41'W, 13 Nov 2003, ex dead twig of woody Asteraceae, montane rainforest, P. S. Ward PSW15038 (USNM) (CASENT0794097). Paratypes. Series of 9 workers, same data as holotype (CASC, JTLC, MCZC, PSWC, UCDC, UVGC).

Other material examined (LACM, MCZC, PSWC, UCDC, UVGC). GUATEMALA Alta Verapaz: 7 km SW Cobán, 1460 m (P. S. Ward); airport near Cobán (D. H. Janzen); Cobán (N. L. H. Krauss); Guatemala: Guatemala, San Isidro, 1615 m (C. Lezama); Guatemala, San Isidro, 1615 m (R. Pérez); Sacatepéquez: Antigua (W. M.

Wheeler); *Sololá*: 1 km N San Andrés Semetabaj, 1840 m (P. S. Ward); *Zacapa*: Santa Clara, interior valley of Sierra de las Minas (N. of Cabañas) (R. D. Mitchell).

Worker measurements (n = 8). HL 1.02–1.08, HW 0.94–0.99, MFC 0.029–0.047, LHT 0.73–0.77, CI 0.90–0.94, REL 0.48–0.51, REL2 0.53–0.56, FCI 0.030–0.047, FI 0.43–0.46, PLI 0.54–0.57, PWI 0.50–0.60.

Worker diagnosis. Medium-sized species (see HL, HW and LHT measurements) with head slightly longer than broad (CI <1.00) and eyes moderately elongate (REL >0.47); anterior margin of median clypeal lobe concave, and laterally angulate; palp formula 5,3; frontal carinae closely contiguous, separated by notably less than basal scape width; profemur relatively robust; mesosoma as in Fig. 3, metanotal groove very weakly impressed, and not evident in lateral view, mesosoma appearing broadly convex in profile; dorsal face of propodeum slightly longer than, and rounding gradually into, declivitous face; petiole as in Fig. 3, a little less than twice as long as high or wide, and with a slightly differentiated anterior peduncle; postpetiole broad, about 1.7–1.8× petiole width. Head, mesosoma and petiole punctulate-coriarious and subopaque; postpetiole and abdominal tergite IV sublucid, their reflectance reduced by fine punctulae and associated dense pubescence. Standing pilosity fine, pale, and somewhat sparse on most parts of the body (MSC 7–12), usually present on the mesonotum but lacking on propodeum. Dark brown, the pronotum—and sometimes the rest of the mesosoma, petiole and appendages—variably lighter brown.

Comments. *P. feralis* can be recognized by the laterally angulate clypeal lobe, moderately long eyes (REL 0.48–0.51), robust profemur (FI 0.43–0.46) and convex mesosomal profile in which the metanotal groove is almost indiscernable. The acacia-ants in the *P. ferrugineus* group have a more slender profemur (FI 0.35–0.41), generally shorter eyes (REL 0.39–0.50), and a well-developed metanotal groove. For distinctions between *P. feralis* and the other non-mutualist in the *P. ferrugineus* group, *P. evitus*, see above under that species. With respect to body size and color, *P. feralis* is superficially similar to a much more common, but undescribed, high-elevation Central American species, *Pseudomyrmex psw159*, which ranges from Chiapas to Nicaragua, and occurs sympatrically with *P. feralis* in Guatemala. *P. psw159* belongs to a distantly related complex of species that includes *P. elongatulus* and *P. championi* (the *P. elongatulus* group, to be treated in a later study). Workers of *P. psw159* can be distinguished from those of *P. feralis* by a number of features, including a laterally rounded median clypeal lobe; 6,4 palp formula; shorter eyes (REL 0.42–0.47); more elongate head (CI 0.82–0.86); and more slender profemur (FI 0.40–0.44).

Distribution and biology. *P. feralis* is apparently restricted to Guatemala where it is associated with montane rainforest and mixed tropical-temperate mesic forest, at elevations ranging from 1460 m to 1900 m. I have collected three nest series, all in dead twigs. The workers are non-aggressive and uninclined to sting.

Key to species of the *P. ferrugineus* group, based on the workers and queens

This key incorporates the two new species into the previously published key for the *P. ferrugineus* group (Ward 1993: 131–132). The latter should be consulted for identification of the remaining species. Sample sizes are given for each set of measurements.

- | | | |
|---|--|---|
| 1 | Eyes more elongate (worker REL 0.48–0.55, n = 22; queen REL 0.47–0.50, n = 4); profemur more robust (worker FI 0.42–0.46, n = 22; queen FI 0.46–0.51, n = 4); worker metanotal groove weakly impressed; dead twig inhabitant | 2 |
| - | Eyes less elongate (worker REL 0.39–0.50, n = 280; queen REL 0.38–0.48, n = 166); profemur more slender (worker FI 0.35–0.41, n = 22; queen FI 0.39–0.44, n = 13); worker metanotal groove well developed; obligate inhabitants of swollen-thorn acacias (<i>Vachellia</i> species) | remaining species; see couplets 11–19 of key in Ward (1993) |
| 2 | Large species (worker HW 1.15–1.28, n = 14; queen HW 1.28, n = 1) with longer legs (worker LHT 0.91–1.00, n = 14; queen LHT 1.04, n = 1) and broader head (worker CI 1.01–1.05, n = 14; queen CI 0.88, n = 1); palp formula 4,3 | <i>evitus</i> |
| - | Smaller species (worker HW 0.94–0.99, n = 8; queen HW 1.01–1.06, n = 3) with shorter legs (worker LHT 0.73–0.77, n = 8; queen LHT 0.80–0.83, n = 3) and more elongate head (worker CI 0.90–0.94, n = 8; queen CI 0.85–0.86, n = 3); palp formula 5,3 | <i>feralis</i> |

Pseudomyrmex goeldii group

This is a small but distinctive group, comprising five known species. The distribution of the clade is centered in South America, but two species have penetrated as far north as Nicaragua and Costa Rica, respectively. Unlike

most species in the *P. ferrugineus* group, the ants of the *P. goeldii* group are generalist inhabitants of dead twigs, and they have a timid demeanor.

Worker diagnosis. Small species (HW 0.47–0.78, HL 0.65–0.93); head longer than broad (CI 0.69–0.85) and eyes strikingly elongate (REL 0.55–0.66). Masticatory margin of mandible with 5–6 teeth; mesial tooth on basal margin about equidistant between apicobasal angle and proximal tooth. Palp formula 5,3 or 4,3. Anterior margin of median clypeal lobe broadly concave, with a weak median protrusion, and with sharp lateral angles. Frontal carinae closely contiguous (FCI 0.010–0.019) and forming a thin anterodorsally elevated ridge, the carinae directed forward onto the median clypeal lobe rather than fusing with the antennal sclerites anterolaterally. Profemur very robust (FI 0.49–0.56). Metanotal groove strongly impressed (Figs 4–8). Dorsal and declivitous faces of propodeum well differentiated; in profile the juncture between the two varying from weakly to strongly angulate, sometimes producing small, paired tubercles. Petiole relatively short (PL/HL 0.35–0.49), longer than high or wide (PLI 0.51–0.80, PWI 0.48–0.66), and without a well differentiated anterior peduncle; anteroventral petiolar tooth present. Postpetiole broader than long, with small anteroventral tooth. Body sculpture varying from smooth and shining, with scattered fine punctulae, to densely punctulate-coriarious or coriarious-imbricate. Standing pilosity very sparse (MSC 0–2), a single pair or none at all on dorsum of head, mesosoma (pronotum), petiole and postpetiole; absent from the extensor faces of tibiae (HTC 0, MTC 0). Appressed pubescence moderately dense on petiole, postpetiole and abdominal tergite IV, variably so on rest of body. Color varying from brownish-yellow to dark brown, often bicolored.

Queen diagnosis. Similar to worker except for caste-specific differences. Head more elongate (HL 0.74–0.97, CI 0.62–0.78); median clypeal lobe more protruding; profemur more robust (FI 0.53–0.59); dorsal face of propodeum shorter than declivitous face, the juncture between the two gently rounded, not angulate. Petiole generally more slender than in worker (PL/HL 0.46–0.51, PLI 0.57–0.67, PWI 0.50–0.58). Forewing with 2 submarginal cells, i.e., cross-vein 2rs-m present.

Male diagnosis. Relatively small species (HW 0.53–0.69, HL 0.58–0.74; n = 4). Head longer than broad (CI 0.88–0.92); compound eye large, prominent (REL 0.55–0.60, REL2 0.62–0.65). Mandibles with about 6–8 teeth or denticles on masticatory margin. Palp formula as in females. Surface of median clypeal lobe convex, its anterior margin subtriangular in shape (dorsal view) with sides converging medially to a rounded point. Scape short (SI 0.20–0.23). Petiole and postpetiole slender (PLI 0.54–0.59, PWI 0.41–0.49). Posterolateral corners of sternites IV–VIII not notably protruding ventrally. Posterior margin of subgenital plate (sternite IX) broadly convex, lacking conspicuous posteromedial concavity. Posterior margin of pygidium (tergite VIII) convex, directed posteroventrally. Paramere with angulate or rounded posterodorsal extremity, and a low angulate mediadorsal lobe (as seen in lateral view) representing the summit of a well-developed mesial dorsoventral ridge. Aedeagus with somewhat expanded posterodorsal corner; posterior margin with numerous small teeth (10+), preceded by a sinuous carina on the outer face of the aedeagus, which converges to the posterior margin dorsally.

Comments. Workers and queens of the *Pseudomyrmex goeldii* group are superficially similar to those of the *P. pallidus* group (as defined in Ward 1989), with which they share a laterally angulate median clypeal lobe and sparsity of standing pilosity on the body. In the *P. pallidus* group, however, the frontal carinae do not form an anterodorsally elevated ridge that is directed forward onto the median clypeal lobe; instead the carinae are directed anterolaterally where they fuse with the antennal sclerites, as in most *Pseudomyrmex*. In addition, in the *P. pallidus* group the dorsal and declivitous faces of the propodeum usually round into one another, rather than meeting at an angle. The unusual configuration of the frontal carinae in the *P. goeldii* group is also seen in the *P. subtilissimus* group (Ward 1989), but in this latter group the median clypeal lobe is laterally rounded, not angulate; the head is distinctly elongate (worker CI 0.56–0.73 versus 0.69–0.85 in the *P. goeldii* group); and there is a characteristic pair of setae on the propodeum at the juncture of the dorsal and declivitous faces.

List of included species

- P. goeldii* (Forel 1912); southeastern Brazil
P. laevifrons Ward 1989; Nicaragua to central Brazil
 = *P. laeviceps* (F. Smith 1877) (preoccupied)
P. micans Ward, sp. nov.; Peru, Bolivia

P. obtusus Ward, sp. nov.; Costa Rica to Peru and Brazil

P. parvulus Ward, sp. nov.; Bolivia, Brazil

Species accounts

Pseudomyrmex goeldii (Forel)

(Fig. 4)

Pseudomyrma goeldii Forel 1912: 28. Syntypes, three workers, Sorocaba, São Paulo, Brazil (Göldi) (MHNG) [Examined] [One syntype worker also imaged on AntWeb: CASENT0907543].

Worker measurements (n = 3). HL 0.81–0.87, HW 0.65–0.66, MFC 0.009–0.010, CI 0.76–0.80, REL 0.55–0.56, REL2 0.69–0.73, FCI 0.014–0.015, FI 0.49–0.53, PLI 0.51–0.59, PWI 0.48–0.56.

Worker diagnosis. Larger species (HL 0.81–0.87, HW 0.65–0.66) in comparison with other members of the *goeldii*-group, with shorter eyes (see REL and REL2 indices); juncture between dorsal and declivitous faces of propodeum only weakly angulate; in profile anterodorsal face of petiole ascending about as steeply as posterodorsal face. Head smooth and shiny with scattered fine punctulae; pronotum similar, but remainder of mesosoma becoming sublucid, with coriarious-imbricate sculpture; luster of petiole, postpetiole and gaster dulled by moderately dense pubescence. Rather uniformly dark brown, appendages slightly lighter.

Comments. This species is distinguished by the combination of relatively large size (HL 0.81–0.87, HW 0.65–0.66), shiny puncticulate head, and weakly angulate juncture of the dorsal and declivitous faces of the propodeum. The eye appears to be shorter than in other members of the *goeldii* group (REL 0.55–0.56 versus 0.57–0.66 in other species; REL2 0.69–0.73 versus 0.75–0.87).

Distribution and biology. *P. goeldii* is known only from the type series collected more than a century ago in southeastern Brazil by Emílio Goeldi. The type locality (Sorocaba) is located within the Atlantic rainforest region.

Pseudomyrmex laevifrons Ward

(Fig. 5)

Pseudomyrma laeviceps F. Smith 1877: 63. Lectotype worker (designated by Ward 1989: 440), Para, Brazil (BMNH) [Examined] [Also imaged on AntWeb: CASENT0902923] [Preoccupied by *Pseudomyrmex laeviceps* F. Smith 1859 =*Tetraponera laeviceps* (F. Smith)].

Pseudomyrmex laevifrons Ward 1989: 440. Replacement name.

Other material examined (ALWC, BMNH, CASC, CPDC, CUIC, FSCA, INBC, INPA, IZAV, JTLC, KWJC, LACM, MCZC, MNHN, MPEG, MZLU, MZSP, PSWC, UCDC, USNM). BOLIVIA Beni: 46 km SSW San Borja, 300 m (P. S. Ward); BRAZIL Amapá: Oiapoque (W. L. Overal); Amazonas: Faz. Esteio, 80 km NNE Manaus, 80 m (P. S. Ward); High Falls, Rio Tarumã (W. L. Brown); Tefé [as "Ega"] (c.u.); Bahia: C. das Almas, Fz. Capivari (M. R. B. Smith); Canavieiras (V. L. Mello); Guarajuba, Camacari (J. Delabie); Ilhéus (V. L. Mello); Ilhéus-Cepec (J. D. Majer); Ilhéus-Cepec (H. J. Santos); Itacaré (V. L. Mello); São Miguel, Ilheus (A. Batista); São Miguel, Ilheus (I. C. Nascimento); Para: Monte Dourado, Area 75 (C. J. Marsh); COLOMBIA San Andrés y Providencia: San Andrés Isla, Massalli Hill (F. Castellanos); COSTA RICA Alajuela: 11 mi N Florencia (D. H. Janzen); Heredia: Est. Biol. La Selva, 50–150 m (INBio/OET); Limón: La Lola (D. H. Janzen); Puntarenas: 19 km S Cuidad Neily, 20 m (P. S. Ward); Sirena, Penin. Osa, 50 m (J. T. Longino); Golfito, 5 m (P. S. Ward); ECUADOR Los Ríos: Jauneche, 19 km WSW Mocache, 60 m (P. S. Ward); Napo: 1 km SW Archidona, W side Río Misahualli, 550 m (A. L. Wild); 3 km NNE Archidona, 650 m (A. L. Wild); Jatun Sacha, 7 km ESE Pto. Misahualli, 400 m (P. S. Ward); Orellana: Tiputini Biodiversity Station (T. Erwin); Sucumbios: Cuyabeno, Destacamento Patria, 200 m (D. A. Donoso); Sacha Lodge [as "Sacha"] (L. Huggert); FRENCH GUIANA Cayenne: Kaw Mountains, 325 m (K. Sarv); Petit Saut [as "Petit Saux"] (Estelle); Sinnamary (G. Délye); Saint-Laurent-du-Maroni: Haut-Itany (R. Garrouste); GUYANA Cuyuni-Mazaruni: Kartabo (W. M. Wheeler); East Berbice-Corentyne: New River, 750 ft. (C. A. Hudson); Essequibo Islands-West Demerara: Timehri, 0–50 m (J. T. Longino); Wales, 0–50 m (J. T.

Longino); NICARAGUA *Madriz*: 12.1 mi N Condega, Hwy. 1 (D. H. Janzen); PANAMA *Colón*: Pipeline Rd. (G. G. Montgomery; Y. Lubin); PERU *Huánuco*: Tingo Maria, Cueva de las Pavas (L. Huggert); *Junín*: Satipo (L. Huggert); *Loreto*: Iquitos, Barillal (L. Huggert); *Madre de Dios*: Cuzco Amazónico, 15 km NE Pto. Maldonado (S. P. Cover; J. E. Tobin); Pakitza, Rio Manu, 250 m (Erwin; Farrell); *San Martín*: 24 km NNE Tarapoto, 220 m (P. S. Ward); Convento, 26 km NNE Tarapoto, 220 m (P. S. Ward); *Ucayali*: Yurac, 67 mi E Tingo Maria (E. I. Schlinger; E. S. Ross); TRINIDAD & TOBAGO: *Couva-Tabaquite-Talparo*: 2 km SE Las Lomas (J. K. Wetterer); *Sangre Grande*: Tapana (J. K. Wetterer); *Siparia*: La Brea (H. Morrison); *Tobago*: 1 1/8 mi ESE Adelphi (P. Feinsinger); *Tunapuna-Piarco*: 2 km E Carmichael (J. K. Wetterer); 2 km NW Howson, (J. K. Wetterer); Heights of Guanapo (J. K. Wetterer); Waller Field, 10 m (P. Feinsinger); Waller Field (J. K. Wetterer); VENEZUELA *Aragua*: Ocumare de la Costa, 20 m (P. S. Ward); *Barinas*: 10 km WNW Santa Barbara, 280 m (P. S. Ward); *Bolívar*: 49 km ENE Tumeremo, 200 m (P. S. Ward); Campamento Río Grande, 250 m (P. S. Ward); Rio Akanan, 470 m (J. Lattke); *Miranda*: Cúpira, 15 m (W. Goitia); Padron, Est. Exp. de Caucagua, ca. R. Tuy & R. Cuira (Brandão et al.); *Trujillo*: 19 km E Boconó, 600 m (P. S. Ward);

Worker measurements (n = 16). HL 0.65–0.75, HW 0.47–0.55, MFC 0.005–0.010, LHT 0.36–0.41, CI 0.69–0.78, REL 0.57–0.64, REL2 0.79–0.87, FCI 0.010–0.019, FI 0.50–0.56, PLI 0.66–0.80, PWI 0.54–0.66.

Worker diagnosis. Small species (HL 0.65–0.75, HW 0.47–0.55) with elongate head and eyes (CI 0.69–0.78, REL 0.57–0.64, REL2 0.79–0.87); masticatory margin of mandible with 5 teeth; palp formula 4,3; juncture between dorsal and declivitous faces of propodeum usually notably angulate, sometimes producing slight tubercles laterally; anterodorsal face of petiole usually ascending relatively steeply (Fig. 5b). Head smooth and shiny with scattered fine punctulae; pronotum similar centrally, but remainder of mesosoma becoming sublucid, with coriarious-imbricate sculpture on most surfaces including mesopleuron, metapleuron and propodeum; petiole, postpetiole and gaster with moderately dense pubescence. Standing pilosity sparse (MSC 2); paired erect setae present on pronotal humeri, petiole and postpetiole. Dark brown, mandibles, frontoclypeal complex and tarsi lighter; pronotum, petiole and postpetiole often a contrastingly lighter medium- to yellowish-brown.

Comments. Workers of this species can be recognized by their small size (HW 0.47–0.55), shiny puncticulate head, angulate propodeum, and the presence of a single pair of erect setae on the pronotal humeri, petiole and postpetiole. *P. obtusus* and *P. parvulus* have a more densely sculptured head and less standing pilosity (lacking at least on the petiole). Differences between *P. laeviceps* and the closely similar *P. micans* are discussed under the latter species.

Distribution and biology. This species is distributed from Nicaragua to Bolivia and central Brazil, and has been recorded from tropical moist forest, rainforest, second-growth rainforest, and rainforest edge. Most collections consist of scattered foragers on low vegetation and on recent treefalls. I have collected seven nest series, all from dead twigs of woody plants: two from vines, three from Melastomataceae trees, and two from unidentified plants.

Pseudomyrmex micans Ward, sp. nov.

(Fig. 6)

Pseudomyrmex goeldii; Chomicki et al. (2015: 4) (misidentification).

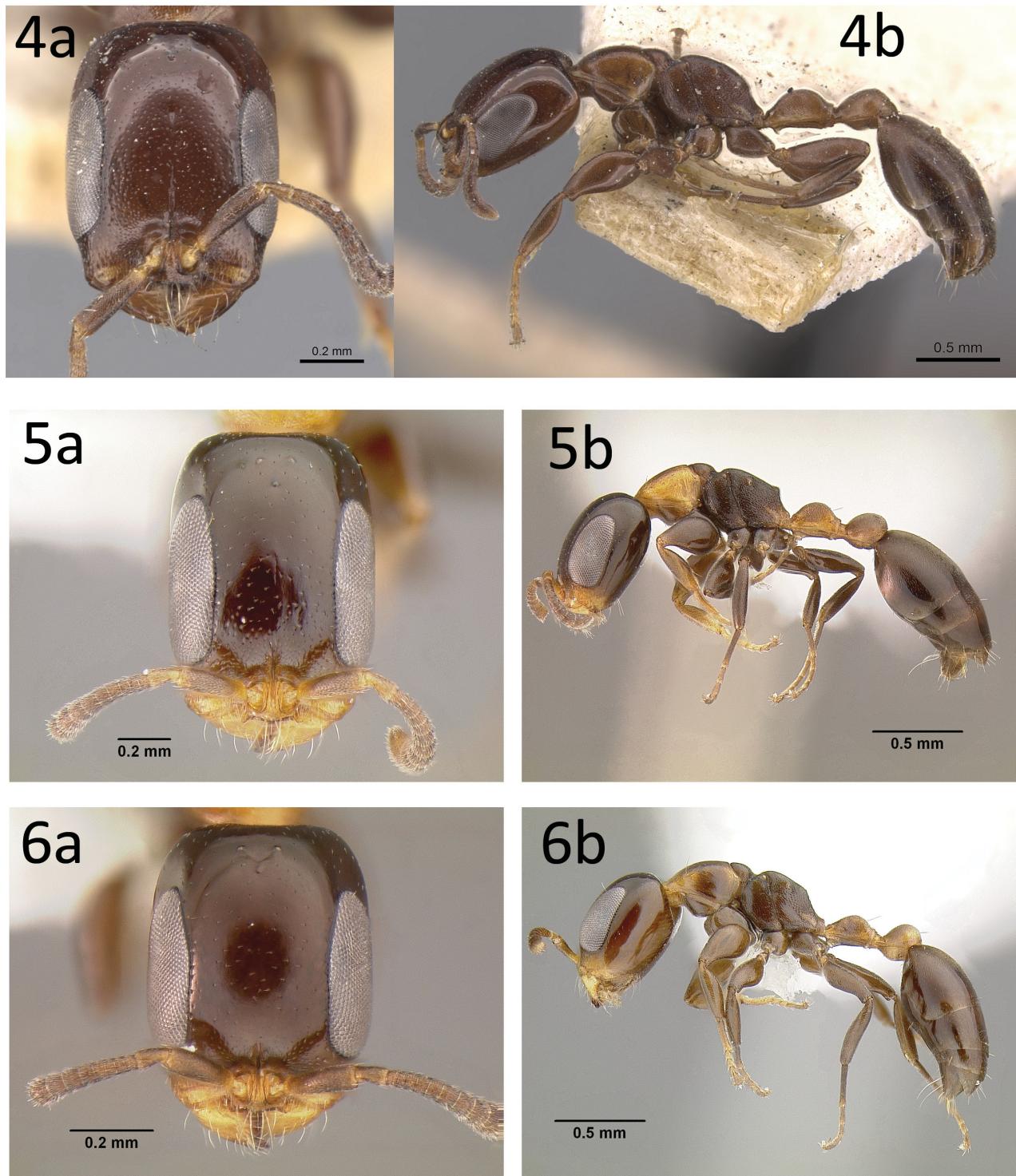
Type material. Holotype worker. PERU *San Martín*: Tarapoto, 350 m, 6°29'S, 76°22'W, 25 Aug 1986, ex dead twig, edge of second-growth rainforest, P. S. Ward PSW08734 (MZSP) (CASENT0794101). Paratypes. Series of workers, 1 male, same data as holotype (CASC, JTLC, MCZC, PSWC, UCDC, USNM).

Other material examined (PSWC). BOLIVIA *Santa Cruz*: 11 km NE Aserradero Moira, 180 m (P. S. Ward).

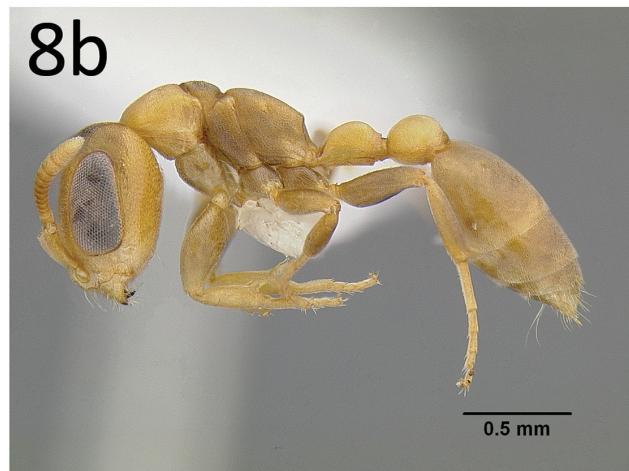
Worker measurements (n = 6). HL 0.67–0.74, HW 0.52–0.55, MFC 0.007–0.009, LHT 0.39–0.42, CI 0.74–0.80, REL 0.59–0.61, REL2 0.75–0.80, FCI 0.013–0.016, FI 0.53–0.55, PLI 0.64–0.69, PWI 0.56–0.63.

Worker diagnosis. Small species (HL 0.67–0.74, HW 0.52–0.55) with elongate head and eyes (CI 0.74–0.80, REL 0.59–0.61, REL2 0.75–0.80); masticatory margin of mandible with 5 teeth; palp formula 4,3; juncture between dorsal and declivitous faces of propodeum only weakly angulate, not producing lateral tubercles; anterodorsal face of petiole ascending gently (Fig. 6b). Head smooth and shiny with scattered fine punctulae; pronotum similar, remainder of mesosoma becoming sublucid, with coriarious-imbricate sculpture on most

surfaces, but with shining areas on the mesopleuron and metapleuron; petiole, postpetiole and gaster with moderately dense pubescence. Standing pilosity sparse (MSC 2); paired erect setae present on pronotal humeri, petiole and postpetiole. Dark brown, mandibles, frontoclypeal complex and tarsi lighter; pronotum, petiole and postpetiole sometimes a lighter medium- to yellowish-brown.



FIGURES 4–6. *Pseudomyrmex goeldii* group, workers, full-face dorsal view of head (a) and lateral profile of body (b). 4, *P. goeldii*, Brazil (CASENT0907543); 5, *P. laevifrons*, Bolivia (CASENT0762973); 6, *P. micans*, Peru (CASENT0794101). Images from AntWeb (www.antweb.org); photographers Will Ericson (4) and Matthew Prebus (5, 6).



FIGURES 7–8. *Pseudomyrmex goeldii* group, workers, full-face dorsal view of head (a) and lateral profile of body (b). 7, *P. obtusus*, Venezuela (CASENT0794100); 8, *P. parvulus*, Brazil (CASENT0762994). Images from AntWeb (www.antweb.org); photographer Matthew Prebus.

Comments. Based on the weakly angulate propodeum this species was initially considered conspecific with *P. goeldii* (and called this in Chomicki *et al.* 2015), but a more careful examination of relevant material reveals substantial differences: *P. micans* is smaller in size (HW 0.52–0.55 versus HW 0.65–0.66 in the three syntype workers of *goeldii*), and has more elongate eyes (REL 0.59–0.61 versus 0.55–0.56), a shorter petiole (PLI 0.64–0.69 versus 0.51–0.59), and a more shiny mesosoma. *P. micans* appears to be closely related to *P. laevifrons*, differing primarily by the less pronounced angular juncture of the dorsal and declivitous faces of the propodeum; by the weaker body sculpture, especially on the metapleuron, which is more strongly shining; by slightly lower REL2 values (see above); and by the shape of the petiole, which is lower, wider, and with a more gently sloping anterodorsal face (compare Figs 5b and 6b). Collections from Peru and Bolivia can be separated into one or the other of these two forms, based on the features listed above. This includes diagnostic differences in petiolar metrics: PLI 0.72–0.80 in *P. laevifrons* ($n = 5$) versus 0.64–0.69 in *P. micans*; DPW/PH 0.76–0.85 in *P. laevifrons* versus 0.88–0.92 in *P. micans*. In other parts of the range of *P. laevifrons*, where *P. micans* is apparently absent, the petiolar diagnostics break down, and some workers show a weakening of the pronounced angle at the juncture of the dorsal and declivitous faces of the propodeum. One interpretation of this pattern is that *P. laevifrons* ranges from Central America to Bolivia and central Brazil, undergoing character displacement where it overlaps with the more southern species, *P. micans*. An alternative hypothesis is that the species are distinct in some areas but that differences are obscured by gene flow elsewhere. The entire complex of populations would benefit from a focused phylogenetic analysis.

Distribution and biology. As currently conceived *P. micans* is known only from rainforest sites in Peru (nest

ex dead twig, edge of second-growth rainforest) and Bolivia (workers foraging on recent *Tabebuia* and *Hymenaea* treefalls).

***Pseudomyrmex obtusus* Ward, sp. nov.**

(Fig. 7)

Pseudomyrmex psw001; Chomicki *et al.* (2015: 4).

Type material. Holotype worker. VENEZUELA Barinas: 10 km WNW Santa Barbara, 280 m, 7°51'S, 71°16'W, 29 Aug 1987, ex dead twig of thorny vine, edge of second-growth rainforest, P. S. Ward PSW09027 (MZSP) (CASENT0794100). Paratypes. Series of workers, 3 dealate queens, same data as holotype (CASC, JTLC, MCZC, PSWC, UCDC, USNM).

Other material examined (LACM, MZSP, PSWC, UCDC). BRAZIL Mato Grosso: Sinop (M. Alvarenga); COSTA RICA Puntarenas: Res. Biol. Carara, 500 m (J. Longino); Reserva Biol. Carara, 500 m (P. S. Ward); PANAMA Colón: Pipeline Rd. (G. G. Montgomery & Y. Lubin); PERU San Martín: 24 km NNE Tarapoto, 220 m (P. S. Ward); SURINAM Para: Zanderij I (Boven); VENEZUELA Barinas: 10 km WNW Santa Barbara, 280 m (P. S. Ward).

Worker measurements (n = 9). HL 0.86–0.93, HW 0.71–0.78, MFC 0.007–0.013, LHT 0.48–0.54, CI 0.80–0.85, REL 0.63–0.66, REL2 0.75–0.81, FCI 0.010–0.017, FI 0.50–0.52, PLI 0.62–0.71, PWI 0.52–0.64.

Worker diagnosis. Larger species (HL 0.86–0.93, HW 0.71–0.78) with elongate eyes (REL 0.63–0.66) and with broader head than other species in the *P. goeldii* group (CI 0.80–0.85); masticatory margin of mandible with 5–6 teeth; palp formula 5,3; juncture between dorsal and declivitous faces of propodeum subangulate, and with conspicuous lateral tubercles (Fig. 7b); anterodorsal face of petiole ascending rapidly, often steeper than posterodorsal face (Fig. 7b). Front of head between eyes densely punctulate and opaque, becoming sparsely punctulate and shiny around the ocelli, then densely punctulate and opaque again at the posterior margin; mesosoma finely coriarious-imbricate and opaque; petiole, postpetiole and gaster with very fine dense pubescence, imparting a matte appearance. Standing pilosity very sparse, absent from mesosoma, petiole and postpetiole. Medium to dark brown, the petiole, postpetiole and most of gaster a contrasting light yellowish-brown; mandibles, frontoclypeal complex, tibiae and tarsi also lighter than most of body, the pronotum variably so.

Comments. Within the *P. goeldii* group this species is recognized by its large size (HW >0.70), broad head (CI >0.79), and dense punctulate sculpture on the front of the head. Other distinctive features are the matte appearance of most of the body and the absence of standing pilosity on the mesosoma, petiole and postpetiole.

Distribution and biology. *P. obtusus* is known from scattered collections from Costa Rica to Peru and Brazil. Collections with habitat information come from rainforest, rainforest edge, and (Costa Rica) successional pasture near rainforest. I have made four nest collections: two from dead twigs of *Ficus* sp., one from a dead twig of a thorny vine, and one from a dead twig of an unidentified woody plant.

***Pseudomyrmex parvulus* Ward, sp. nov.**

(Fig. 8)

Type material. Holotype worker. BRAZIL Amazonas: Paraná do Xiboreninho, 3°15'S, 60°00'W [mistranscribed on label as 06°00'W], 5 Aug 1979, Canopy Fogging Project, TRS#05, mixed water, Adis, Erwin, Montgomery *et al.* (MZSP) (CASENT0794102). Paratypes. 1 worker same data as holotype (PSWC) (CASENT0762994); 1 worker, BRAZIL Amazonas: Rio Tarumã Mirim, 2 km from Rio Negro, 3°02'S, 60°17'W, 27 Jul 1979, Canopy Fogging Project, TRS#01, black water inundation forest, Adis, Erwin, Montgomery *et al.* (USNM) (CASENT0794103).

Other material examined (UCDC). 1 dealate queen, BOLIVIA Santa Cruz: 35 km SSE Flor de Oro, 450 m (P. S. Ward PSW12198-06).

Worker measurements (n = 3). HL 0.73–0.80, HW 0.56–0.60, MFC 0.005–0.007, LHT 0.40–0.43, CI 0.75–0.78, REL 0.64–0.65, REL2 0.82–0.86, FCI 0.009–0.012, FI 0.52, PLI 0.63–0.71, PWI 0.52–0.60.

Worker diagnosis. Smaller species (HW 0.56–0.60) with moderately elongate head and eyes (CI 0.75–0.78, REL 0.64–0.65); palp formula 5,3; juncture between dorsal and declivitous faces of propodeum subangulate, and with weak lateral tubercles (Fig. 8b); anterodorsal face of petiole ascending rapidly (Fig. 8b). Front of head between eyes densely punctulate and sublucid, the punctures separated by about their diameters; head sparsely punctulate and shiny around the ocelli, then more densely punctulate and sublucid at the posterior margin; mesosoma finely coriarious-imbricate and largely opaque; petiole, postpetiole and gaster with very fine dense pubescence, imparting a matte appearance. Standing pilosity very sparse, absent from petiole; a pair of setae present on the pronotal humeri and on the postpetiole (latter pair very short and inconspicuous). Medium yellowish-brown, the pronotum, petiole, postpetiole and appendages lighter.

Comments. In this species the head is densely punctulate between the compound eyes and most of the body has a matte texture. In this respect *P. parvulus* is similar to *P. obtusus*, but it is smaller in size (HW 0.56–0.60, with a more elongate head (CI 0.75–0.78) and a pair of setae on the pronotal humeri (absent in *P. obtusus*).

Distribution and biology. *P. parvulus* is known only from two rainforest sites in Amazonas, Brazil (workers from canopy fogging project), and one rainforest location in the Sierra de Huanchaca, Bolivia (dealate queen on low vegetation).

Key to species of the *P. goeldii* group, based on the workers and queens

This key summarizes the differences discussed above. Sample sizes of measurements are given (e.g., n = 5). Unless otherwise noted, sample sizes are the same for all measurements of a given caste cited within any particular lug of a couplet.

- 1 Front of head between compound eyes densely punctulate, the punctures separated by their diameters or less, becoming smooth and sparsely punctulate around the ocelli; mesosoma with dense coriarious-imbricate sculpture, and wholly opaque; petiole without erect setae 2
- Front of head smooth, shiny, and sparsely puncticulate; mesosoma less densely sculptured, appearance shinier, especially on the pronotum; petiole with a pair of erect setae 3
- 2 Larger species (worker HW 0.71–0.78, n = 9; queen HW 0.70–0.73, n = 3) with broader head (worker CI 0.80–0.85, queen CI 0.75–0.78); standing pilosity absent from mesosoma; Costa Rica to Peru and Brazil *obtusus*
- Smaller species (worker HW 0.56–0.60, n = 3; queen HW 0.58, n = 1) with a more elongate head (worker CI 0.75–0.78, queen CI 0.68); standing pilosity present on the mesosoma as a single pair on the pronotal humeri; Brazil, Bolivia *parvulus*
- 3 Larger species (worker HW 0.65–0.66, n = 3; queen unknown, but expected to have similar HW) with shorter eyes (worker REL 0.55–0.56; worker REL2 0.69–0.73); southeastern Brazil *goeldii*
- Smaller species (worker HW 0.47–0.55, n = 22; queen HW 0.49–0.54, n = 9) with more elongate eyes (worker REL 0.57–0.64; worker REL2 0.75–0.87; queen REL 0.55–0.61; queen REL2 0.80–0.90); Nicaragua to Bolivia and central Brazil 4
- 4 Mesosoma sculpture weaker, especially on the metapleuron, which is partly smooth and shining; juncture of the dorsal and declivitous faces of the propodeum subangulate in worker; petiole relatively low and broad (worker PLI 0.64–0.69, DPW/PH 0.88–0.92; n = 6) and with anterodorsal face more gently sloping than posterodorsal face (Fig. 6b); worker REL2 0.75–0.80; Peru, Bolivia *micans*
- Mesosoma sculpture better developed, the metapleuron coriarious-reticulate and subopaque, smooth shiny patches less well developed; in areas of apparent overlap with *P. micans* (Peru and Bolivia) worker propodeum more strongly angulate, and petiole shorter and higher (worker PLI 0.72–0.80, DPW/PH 0.76–0.85; n = 5), with more steeply sloping anterodorsal face (Fig. 5b); elsewhere worker propodeal angles and petiole shape more variable but tending in the same direction; worker REL2 0.79–0.87 (n = 16); Nicaragua to Bolivia and central Brazil *laevifrons*

Concluding remarks

The *Pseudomyrmex* species that are the subject of this study exemplify several features of evolution in the genus. The *P. ferrugineus* group provides a striking example of convergent evolution of worker morphology among two separate lineages of ant-plant specialists (Ward & Branstetter 2017). The presence of more generalized (non-mutualist) species in the *P. ferrugineus* group necessitates a more nuanced worker-based diagnosis of the clade. The male diagnosis is less affected because features of the males, including genitalia, are shared among all species, both generalists and specialists. In effect, the male morphology better reflects phylogenetic relationships than worker morphology. The *P. goeldii* group, closely related to the *P. ferrugineus* group, comprises only five species,

all apparently generalist dead twig inhabitants. Two of those species (*P. laevifrons*, *P. micans*) exhibit complex patterns of variation, however. They appear to be distinct where occurring sympatrically in Peru and Bolivia, but elsewhere, where only one of the two species is apparently present, there is increased variability. This suggests the possibility of character displacement and/or incomplete reproductive isolation between the two, hypotheses that could be investigated with more detailed genetic studies.

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